purity. And back of this is an obscure history for the material with no evidence it seems to me that *Lamarckiana* was ever present as a native species of any flora. The chief value which the study of my *Lamarckiana*-like hybrid may have for the problem of the origin and status of *Œnothera Lamarckiana* is likely to be a clearer understanding of how an obviously impure species, *neo-Lamarckiana,* may arise, a species which seems likely to present a breeding behavior parallel to that of *Lamarckiana,* and most important of all the significance of sterility in the working out of these results. It appears to me a matter of no vital importance to the status of a hybrid whether its parents are pure or impure. If markedly impure the problem of analysis for future generations merely becomes the greater. Since no species of *Œnothera* has as yet passed the tests for a pure species, we are at present in all of the *Œnothera* work talking of an abstraction when this concept is considered.

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STATISTICAL STUDIES OF THE NUMBER OF NIPPLES IN THE MAMMALS

IT is perhaps not unnatural that a subject of such fundamental interest as that of the nourishment of the young in the mammals should have attracted the attention of observers from the time of the Greek philosophers. It is only within the last few years that attempts have been made to solve various problems by the application of the statistical method to series of quantitatively recorded data.

The materials may be divided for convenience of review.

TYPE, VARIATION AND CORRELATION IN NUMBER OF MAMMÆ

The statement made by Parker and Bullard,[1] on the basis of their splendid series of data for swine, that the standard deviation of the number of nipples is 0.6906 in the males and 0.7905 in the females at once arouses the suspicion of a biometrician. The constants actually are:

[1] Parker, G. H., and C. Bullard, "On the Size of Litters and the Number of Nipples in Swine," *Proc. Amer. Acad. Arts and Sci.,* 49: 399–426, 1913.

	For Males	For Females
Mean	12.4365 ± .0182	11.9077 ± .0159
Standard Deviation	1.4800 ± .0128	1.2803 ± .0112
Coefficient of Variation	11.901 ± .105	10.752 ± .096

Thus instead of the females being "over 14 per cent. more variable than the males" they are in absolute terms actually .1997 ± .0175, or over 13 per cent., *less* variable. Relative variability as measured by the coefficient of variation is 1.149 ± .142 per cent. lower in the female that it is in the male. This lower variability of the female is also quite in evidence if the materials be split up into groups with regular and irregular arrangement of the nipples. Thus:

FOR "REGULAR" CLASS

Males	$\sigma = 1.485 \pm .017$,	C. V. = 12.03 ± .14
Females	$\sigma = 1.315 \pm .021$,	C. V. = 11.16 ± .13
Difference	0.170 ± .027,	0.87 ± .19

FOR "IRREGULAR" CLASS

Males	$\sigma = 1.461 \pm .020$,	C. V. = 11.61 ± .16
Females	$\sigma = 1.210 \pm .016$,	C. V. = 10.02 ± .14
Difference	0.251 ± .026,	1.59 ± .21

However measured, the variability of the number of nipples in the female is always significantly less, *not greater,* than in the male.

Furthermore a rather noteworthy sexual differentiation seems so far to have escaped notice. The mean number of nipples for male pigs is in all cases higher than that for female pigs. Thus:

ALL PIGS

Males	12.4365 ± .0182
Females	11.9077 ± .0159
Difference	0.5288 ± .0242

CLASSIFIED AS REGULAR		CLASSIFIED AS IRREGULAR	
Males	12.3425 ± .0233	Males	12.5833 ± .0234
Females	11.7849 ± .0214	Females	12.0777 ± .0232
Difference	0.5576 ± .0316	Difference	0.5056 ± .0330

In all cases the males have on the average more nipples than the females. The regularity of the differentiation is brought out

by the accompanying table in which actual values have been reduced to *per mille* frequencies. Pigs with 12 nipples or fewer are preponderantly females; pigs with 13 nipples or more are preponderantly males.

Number of Nipples	Male	Female	Difference
8	.0	.3	+ .3
9	.6	1.7	+ 1.1
10	90.6	143.7	+ 53.1
11	162.7	217.9	+ 55.2
12	332.0	370.0	+ 38.0
13	167.6	154.5	— 13.1
14	163.4	82.8	— 80.6
15	49.3	20.0	— 29.3
16	29.8	7.1	— 22.7
17	3.0	1 7	— 1.3
18	1.0	.3	— .7
	1000.0	1000.0	

The correlation between the number of nipples on the two sides are:

Males	.6359 ± .0073
Females	.5419 ± .0088
Difference	.0940 ± .0114
All Pigs	.6063 ± .0055

The correlations are fairly high. Those for males seem to be slightly larger than those for females.

CORRELATION BETWEEN THE NUMBER OF THE YOUNG IN THE LITTER AND THE NUMBER OF MAMMÆ IN THE DAM

The relationship between the number of young per litter and the number of mammæ in the female has at various times aroused considerable interest. As Pearl[2] has pointed out, two kinds of correlation are to be recognized. First, interracial correlation, that between the mean size of the litters and the mean number of mammæ in the females of a series of races or species. Second, intraracial correlation, that between the number of mammæ in an individual mother and the number of young that she bears.

It is the rather obvious interracial correlation that has given rise to such statements as that of Gegenbaur: "Die Zahl der Zitzen steht in inniger Beziehung zur Menge der Jungen." It

[2] Pearl, R., "On the Correlation between the Number of Mammæ of the Dam and Size of Litter in Mammals. I. Interracial Correlation," *Proc. Soc. Exp. Biol. Med.*, 11: 27–30, 1913.

was the problem of intraracial correlation with which Alexander Graham Bell[3] was dealing when he studied the fertility of the multi-nippled race of sheep at Beinn Bhreagh.

Notwithstanding the simplicity of the biological problem a certain amount of confusion seems to have arisen. Thus Parker and Bullard (*loc. cit.*) state:

> It is the chief object of our paper to discuss the relation of the size of litters to the number of nipples in the domesticated swine, *Sus scrofa Linn.*

But instead of determining the correlation between the number of teats of the sow and the number of her young they have actually calculated the relationship between the number of siblings in the litter in which a pig was born *and the number of nipples which she herself possesses!* Surely it should not require specialization in animal behavior to convince one that the teats which are of real service to a young pig are not its own, but those of its mother!

Pearl[4] has quite correctly determined the correlation between the number of nipples in the individual mothers and the number of young in their litters. This he finds to be very low,[5] $r = 0.195 \pm .086$.

It is rather difficult to agree with Pearl in his statement that

> It would seem, *a priori*, that natural selection should have operated to bring about a high correlation, both intra- and inter-racial between these two variables, size of litter and number of mammæ in the dam.

There seems no reason whatever to suppose that natural selection would tend to produce a correlation between the number of mammæ in the mother and the size of her litters *within a race, providing it has produced an average number of nipples suffi-*

[3] Bell, Alexander Graham, *Science*, N. S., 9: 637–639, *pl. 5*, 1899; *loc. cit.*, 19: 767–768, 1904; *loc. cit.*, 36: 378–384, 1912.

[4] Pearl, R., "On the Correlation between Number of Mammæ of the Dam and Size of Litter in Mammals. II. Intraracial Correlation in Swine," *Proc. Soc. Exp. Biol. Med.*, 11: 31–32, 1913.

[5] Wentworth (*Jour. Agr. Res.*, 5: 1148, 1916) records another very low coefficient on unpublished data, but does not state specifically whether it is between the number of mammæ of the mother and the number of her young as in Pearl's series, or between the number in a litter (weighted with their own number) and number of nipples in the individual pigs, as in the series of Parker and Bullard.

ciently large to maintain the race.[6] On the contrary, any theory of ontogeny or phylogeny which demands the existence of a mechanism to provide an embryo pig with the particular number of nipples which would agree closely with the number of young she may be destined to bear as an adult would seem to be not merely cumbersome, but unnecessarily teleological. Since male pigs have more mammæ than females, the cost to the organism is apparently not prohibitive! What one should expect as the result of the action of natural selection would, therefore, not be the development of a regulative mechanism to provide the mother with a number of nipples in close agreement with the size of her future brood, but the development of a number of nipples sufficiently large for the needs of the race.

Pearl's own data show only 7 out of 57 "disadvantageous" combinations, and the table as it stands takes no account of early deaths.[7] Furthermore, his series is small, only 57 individuals, and apparently hardly typical of swine as a class. Parker and Bullard on the basis of a thousand litters show that the (empirical) modal number of nipples is twice the modal number of young, and that the average number of nipples is much more nearly twice the number of young than in Pearl's short series. Thus the data of both Pearl and Parker and Bullard indicate in the words of the latter authors that "disadvantageous combinations in which the number of young pigs outrun the provision for

[6] Natural selection can not be expected to accomplish more for the development of any character than to bring it to and maintain it at a stage of development necessary for the survival of the species in competition with others. That correlation between the number of the young and the number of nipples is not necessary under conditions of domestication is shown by the classic observations of Minot on the guinea pig (*Jour. Phys.*, 12: 103, 1891) in which he pointed out that in his studies 143 litters showed a variation of from 1 to 8 in the number per litter, with a model frequency on 2 and an average of 2.5, although the number of developed mammæ is two.

That the number of young born may regularly exceed the number of nipples in a species persisting under natural conditions is shown by the recent studies of Hill and O'Donaghue on the marsupial *Dasyurus viverrinus* (*Quart. Jour. Micr. Sci.*, N. S., 59: 133–173, 1914) in which they have shown that a remarkable number of eggs are discharged from the ovary at each ovulation and that as a rule more young are borne than can possibly survive because of the limited accommodation of the pouch.

[7] Unfortunately trustworthy figures showing directly the mortality of new-born or recently born pigs seem not to be available. That such mortality is considerable is indicated by certain of the figures given for another purpose by Evvard.

milk, cannot be of frequent occurrence.'' The development of just such a ''factor of safety'' and not the origination of an intraracial correlation is, as emphasized above, just what one would expect of natural selection.

Natural selection, if operative, should, however, bring about an interracial correlation, and this is exactly what observant biologists have always noted and Pearl has expressed statistically by the value $r = .594 \pm .046$, with non-linear regression—a value distinctively higher than that for the intraracial relationship. Thus, as far as they go, these observations instead of evidencing against natural selection, actually show the very conditions to exist which might be expected as the result of the action of this factor of organic evolution.

Inheritance of Number and Arrangement of Nipples in Swine

Attempts at the Mendelian analysis of inheritance of number and arrangement of mammæ in swine have been made by Wentworth,[8] who has suggested that the presence of rudimentary nipples is a sex-limited,[9] sex-linked,[10] or sex-limited[11] character. His final stand is that the pair of rudimentaries posterior to the inguinal pair behave as a Mendelian unit character in heredity, but that somatically it develops in males, which are *RR* or *Rr*, but in the females only when they are *RR*, where *R* indicates the presence and *r* the absence of the factor for rudimentaries.

It is interesting to return to the sexual dimorphism with respect to number of mammæ demonstrated above on the basis of Parker's and Bullard's splendid series of data and to consider it in connection with the hypothesis advanced by Wentworth.

Pearson many years ago showed[12] that with continued random mating the distribution in any generation subsequent to an original random pairing of *RR* and *rr* individuals is

$$\tfrac{1}{4}RR + \tfrac{1}{2}Rr + \tfrac{1}{4}rr.$$

[8] Wentworth, E. N., ''Inheritance of Number of Mammæ in Swine,'' Rep. Am. Breed. Ass., 8, 1912.

[9] Wentworth, E. N., ''Another Sex-limited Character,'' *Science*, N. S., 35: 986, 1912.

[10] Wentworth, E. N., ''Sex-linked Factors in the Inheritance of Rudimentary Mammæ in Swine,'' *Proc. Iowa Acad. Sci.*, 21: 265–268, 1914.

[11] Wentworth, E. N., ''Rudimentary Mammæ in Swine a Sex-limited Character,'' *Science*, N. S., 43: 648, 1916.

[12] Pearson, K., *Phil. Trans. Roy. Soc. Lond., A*, 203: 59–60, 1904.

Both Pearl[13] and Jennings[14] have followed him in this point. If the thousand litters studied by Parker and Bullard come from a population homozygous and heterozygous with respect of a pair of rudimentary nipples in the 1:2:1 proportion and mating at random,[15] then three out of four males as compared with one out of four females should, if Wentworth's hypothesis be correct, show the pair of rudimentaries. Thus the average number of mammæ in the males should be 1 higher than in the females. As a matter of fact it is .529 ± .024 higher.

Further discussion on the basis of the present data would of course be idle.

In his largest paper Wentworth[16] has presented data which indicate sensible parental and grandparental correlations for number of mammæ. In view of the irregularity of the frequency distributions due to the modes on the even numbers and the smallness of the series, as well as the fact that the number of boars was very limited, little weight is to be given to the exact numerical values of his coefficients.

A more detailed analysis of the extensive series of data collected by Parker and Bullard may throw considerable light upon the problem of inheritance. The results must be expressed in terms of fraternal or sororal correlation. Those who are so obsessed with Mendelian theory that they are unwilling to learn anything about a series of data for which their method fails, should discontinue the reading of this review at this point.

Correlation between the number of nipples in siblings may be very readily found by means of intra-class correlation formulæ[17] involving first and second moments for the individual classes (litters).

Let x_m be the number of nipples in a male, x_f the number of nipples in a female pig, n_m the number of males and n_f the number of females in a litter of $n_m + n_f = n$ individuals. Let Σ denote summation within the litter and S a summation for litters. For any litter the moments are therefore $\Sigma(x_m)$, $\Sigma(x_m{}^2)$, $\Sigma(x_f)$,

[13] Pearl, R., AMER. NAT., 47: 606–609, 1913.

[14] Jennings, H. S., *Genetics*, 1: 64, 1916.

[15] Random mating of course applies only to the particular character in question, which is one which would hardly be consciously selected by any breeder.

[16] Wentworth, E. N., "Inheritance of Mammæ in Duroc Jersey Swine," AMER. NAT., 47: 257–278, 1913.

[17] Harris, J. Arthur, *Biometrika*, 9: 446–472, 1913.

$\Sigma(x_f^2)$. Since in a symmetrical intra-class correlation table the variates are weighted in an $(n-1)$-fold manner the fraternal correlation for males is given at once by direct summation from the data table of Parker and Bullard by the formula, written for simplicity in an entirely unreduced form,

$$r = \frac{\dfrac{S[\Sigma(x_m)]^2 - S\Sigma(x_m^2)}{S[n_m(n_m-1)]} - \left(\dfrac{S[(n_m-1)\Sigma(x_m)]}{S[n_m(n_m-1)]}\right)^2}{\dfrac{S[(n_m-1)\Sigma(x_m^2)]}{S[n_m(n_m-1)]} - \left(\dfrac{S[(n_m-1)\Sigma(x_m)]}{S[n_m(n_m-1)]}\right)^2},$$

or substituting actual values

$$r_{x_{m1}x_{m2}} = .323 \pm .019.$$

Apparently complex, the formula is really on closer inspection very simple indeed.

One altogether similar for the females gives the sororal correlation

$$r_{x_{f1}x_{f2}} = .373 \pm .018.$$

Thus the correlation for the females is $.050 \pm .026$ higher than that for the males.

For the cross correlations, that between number of nipples borne by male and female pigs of the same litter, the constant is given by

$$r = \frac{\dfrac{S[\Sigma(x_m)\Sigma(x_f)]}{S(n_m n_f)} - \dfrac{S[n_f\Sigma(x_m)]}{S(n_f n_m)} \times \dfrac{S[n_m\Sigma(x_f)]}{S(n_m n_f)}}{\sqrt{\dfrac{S[n_m\Sigma(x_f^2)]}{S(n_m n_f)} - \left(\dfrac{S[n_m\Sigma(x_f)]}{S(n_m n_f)}\right)^2}\sqrt{\dfrac{S[n_f\Sigma(x_m^2)]}{S(n_f n_m)} - \left(\dfrac{S[n_f\Sigma(x_f)]}{S(n_f n_m)}\right)^2}}$$

or

$$r_{x_m x_f} = .287 \pm .020,$$

a value apparently distinctly lower than that for either males or females alone.

If the correlation between the siblings be determined *irrespective of sex* the value is

$$r = \frac{\dfrac{S[\Sigma(x)]^2}{S[n(n-1)]} - \left(\dfrac{S[(n-1)\Sigma(x)]}{S[n(n-1)]}\right)^2}{\dfrac{S[(n-1)\Sigma(x^2)]}{S[n(n-1)]} - \left(\dfrac{S[(n-1)\Sigma(x)]}{S[n(n-1)]}\right)^2},$$

where the n and x without subscripts denote number of individuals per litter and number of nipples per individual, without reference to sex. Numerically

$$r_{x1x2} = .305 \pm .019.$$

This is lower than the relationship for either of the sexes individually considered, just as one might have predicted on *a priori* grounds from the low value of the cross correlation and from the differentiation in the number of mammæ in male and female pigs.[18]

The correlation coefficients here given show that there is a very material degree of resemblance with respect of nipple number in pigs from the same litter.[19] Indeed the correlation is about one third of the maximum value. Such correlation can be due only to differences in intra-uterine environment or to a strong inheritance of nipple number. The latter seems by far the more probable explanation.

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[18] Harris, J. Arthur, "On Spurious Values of Intra-class Correlation Coefficients Arising from Disorderly Differentiation within the Classes," *Biometrika,* 10: 412–416, 1914.

[19] These values of the fraternal correlation will be but slightly influenced by the weighting of the individuals in the determination of the correlations, since nipple number is but slightly correlated with number in the litter.